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Devonian history of diversity of the rugosan *Cyathaxonia* fauna

TOMASZ WRZOLEK



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Literature data indicate above average diversity of the *Cyathaxonia* fauna in the Devonian period, both in absolute numbers of (sub)families and genera per age and also with respect to taxonomic diversities as calculated per Ma (10^6 years). The Emsian and Famennian faunas, although represented by most numerous (sub)families and genera, have less than average diversities, due to their more than average durations, whereas the shorter intervals of the Pragian and Givetian have the highest values for diversity per Ma, and Frasnian faunas the lowest diversities, for both (sub)families and genera. The post-Givetian crisis may have been responsible for the Frasnian minimum, although limited temporal resolution of the analysis does not allow for a more precise description of the Givetian/Frasnian transition. However, “silent taxa” are extremely numerous in the Frasnian, i.e., taxa which are present both prior to and after the Frasnian, but missing from the Frasnian record itself indicating that the Famennian *Cyathaxonia* fauna contains significant numbers of Lazarus and/or Elvis taxa.

Key words: *Cyathaxonia* fauna, Devonian, Givetian–Frasnian crisis, “silent taxa”.

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Introduction

The term “*Cyathaxonia* fauna” was introduced by Hill (1938–1941) for the simple-structured, mostly non-dissepimentate corals, inhabiting deeper marine settings. Thus the *Cyathaxonia* fauna encompasses morphologically simple tetracorals, of various taxonomical affinities, possibly of similar ecological requirements. It may be a convenient term for descriptive purposes, and, potentially, a useful tool for recognition of some environmental perturbations. On the other hand, strictly monophyletic groups may be morphologically disparate and less informative with regard to ecological questions.

The term is widely used, though the ecological generalization of Hill (1938–1941) has been criticized by Fedorowski (1979), who noted that the many fossils of this fauna occur in shallow-marine habitats as well as in deep-water ones. Fedorowski (1979: 55) also suggested that “*Cyathaxonia* fauna” is synonymous with “monozonate corals”, but this suggestion is not followed here as is reflected by the omission of families with large-sized monozonate solitary genera from the current study.

In a note on the Holy Cross *Cyathaxonia* fauna, Wrzolek (1999) suggested that the diversity of these corals was most strongly influenced by the post-Givetian event (see also Scrutton 1988: 65) while tetracorals of more complex structure and larger size of corallites were most affected by the end-Frasnian crisis (Sorauf and Pedder 1986). The present paper attempts to evaluate this hypothesis on the basis of improved data on the stratigraphic distribution of families and genera of the *Cyathaxonia* fauna obtained from the literature.

Methods

Taxonomy.—Data were collected at two taxonomic levels: family (plus subfamily) and genus. Families and subfamilies listed by Hill (1981) were selected if they met, to a greater or lesser degree, the morphological criteria of the *Cyathaxonia* fauna: 1) solitary, 2) non-dissepimentate, and 3) small-sized. The use of these criteria requires some additional explanation. The *Cyathaxonia* fauna is a gradational group and there are numerous instances, when its unambiguous distinction is impossible. For example, with regard to their solitary nature, some typically solitary species of the *Cyathaxonia* fauna on occasion show peripheral rejuvenation (e.g., rare specimens of *Syringaxon bohemicus* from the Holy Cross Eifelian). This indicates some potential for development of incipient colonies: not phaceloid, but at most weakly dendroid in form. As to their non-dissepimentate character, occasionally the presence of presepiments can be observed, and it is commonly associated with rejuvenation. Also, rarely true dissepiments can be seen in some genera, such as *Guerichiphyllum*. With regard to size, the author knows of no precisely defined size classes in the Rugosa, but the adjectives “small” or “large” are commonly employed, as in definition of the term *Cyathaxonia* fauna. To achieve a level of consistency, in this study small corallites are defined as those less than 1 cm in diameter, medium corallites range from one to 2.5 cm, and large corallites are larger than 2.5 cm in diameter. Some caveats must be mentioned regarding this classification including: 1) presence of specimens of various size within a species, 2) presence of various sized species within a genus, 3) changing taxonomic concepts causing

change of size classification, and also 4) unknown or poorly known magnification of some illustrated material.

Using the above criteria 31 families and subfamilies were selected (Appendix 1). Taxonomic and stratigraphic data were taken mostly from Hill (1981) and modified with data of Nudds and Sepkoski (1993). Though Hill (1981) generally used series rather than stage resolution, while Nudds and Sepkoski (1993) used stages, an important advantage of Hill's data is that it includes barren intervals, i.e., "silent taxa" in the nomenclature proposed here.

In summary, only palaeocyclusids were selected from the order Cystiphyllida; taxa selected from the order Stauriida include: 13 (sub)families belonging to the suborder Metriophyllina (numbers 2 to 14 in Appendix 1; all the families and subfamilies of this suborder), five families and subfamilies belonging to the suborder Stereolasmatina (numbers 15 to 19; all families) and 12 to the suborder Plerophyllina (numbers 20 to 31; also all the families of the suborder). Thus as defined here the *Cyathaxonia* fauna is not a monophyletic group of corals, but rather a group consisting of a wide range of rugosans (?evolved many times, independently), at least in the scheme of Hill (1981).

The analysis conducted at the genus level was limited to the Devonian stages/ages. In this analysis, all the Devonian genera of the *Cyathaxonia* fauna were included, together with those genera present immediately before the Devonian (Upper Silurian), and those present after the Devonian (Early Carboniferous epoch). Thus, a total of 79 genera (listed in Appendix 3) were included in this part of the study belonging to 28 of the 31 (sub)families of the family-level analysis. The temporal distribution data were derived primarily from Oliver and Pedder (1979), and improved with data from Hill (1981), and from more recent literature (Appendix 3).

Stratigraphy.—The temporal focus of the present study is the Devonian period and the divisions of the Devonian employed were as fine as possible (stages). For the other systems, which are only presented as background for the Devonian, mostly series were used. Because of the lack of sufficiently precise stratigraphic data, ages rather than chrons were used in the present study, although in rare instances and for narrow intervals better resolution data also are available (as in Scrutton 1988: chrons of the Frasnian to Tournaisian interval). A better understanding of the diversity dynamics of fossil taxa could be gained by more reliable and more precise stratigraphic resolution. In this respect, better stratigraphic data may be expected for the *Cyathaxonia* fauna as in the Devonian it is usually reported from open-marine habitats which contain abundant pelagic fossils of high stratigraphic value.

In the analysis, absolute numbers of taxa in a given chronostratigraphic interval were normalized to the interval duration, such the diversities are presented as number of taxa per Ma (10^6 years; Appendices 2 and 4). Interval durations were based on radiometric data reported in McKerrow and Van Staal (2000: table 1).

Results

The diversity data are presented in form of bar diagrams. Width of a bar is proportional to duration of a particular interval, its height indicates diversity calculated per Ma. Because the records of some taxa contain gaps, i.e., intervals during which the taxon has not been recorded, diversity counts will differ depending on whether only observed taxa are counted ("raw" counts of Olszewski and Patzkowsky 2001) or whether a "range-through" method is applied. In this study the total height of a bar represents diversities based on the "range through" method (Olszewski and Patzkowsky 2001: 649), i.e. it takes into account all taxa present below and above the given interval rather than only those actually reported from the interval. Taxa are identified as "present" and "dubious" in the lower parts of bars ("dubious" records are those for which doubts concern stratigraphy rather than taxonomy). At the top of some bars are the "silent taxa" corresponding to difference between higher value of "range through" and lower value of "raw" diversity, and indicating the "missing" records in some intervals: this will be discussed in the section "silent taxa".

Family and subfamily level diversity (Fig. 1, derived from Appendix 2).—The Caradoc–Llandovery interval has a very low diversity of the *Cyathaxonia* fauna, with subsequent increase during the Wenlock, and with more than average diversity (which is $206/214 = 0.96$ records per Ma on average) in the Upper Silurian and the Devonian. The Pragian and Givetian show rather low absolute numbers of families (subfamilies), but when normalized for interval duration, actually exhibit diversity maxima—due to their shorter than average durations. On the other hand, the longer than average durations of the Emsian and Famennian (15.5 and 14.5 Ma respectively), result in these two intervals representing Devonian minima of diversity, even though both have large absolute numbers of (sub)families. The Frasnian shows high diversity only in the "range through" method: in fact there are more silent than present ("raw") taxa in this interval (8 vs. 5 in absolute numbers, 1.33 vs. 0.84 per Ma). This is an exceptionally high ratio. As noted below this may reflect either poor recognition of Frasnian *Cyathaxonia* fauna or the consequences of the Givetian–Frasnian crisis in this group (or both). The other significant patterns in the record of Devonian diversity are the much higher diversities in the Pragian than in the Emsian (roughly three times fewer families in the latter) and, similarly, in the Famennian than in the Tournaisian.

Generally, the Upper Paleozoic is characterized by lower family diversities of the *Cyathaxonia* fauna, although the Viséan and the Upper Carboniferous have higher than average diversities. Also, Fedorowski (1989: fig. 1) presented data that indicate an extraordinarily high peak of diversity of the *Cyathaxonia* fauna in the *Neoschwagerina* plus *Lepidolina*–*Yabeina* interval (approximately Ufa and Kazan, ca. 5 Ma duration) in the Tethyan Realm. Although no exact numbers of families and genera are provided by Fedorowski

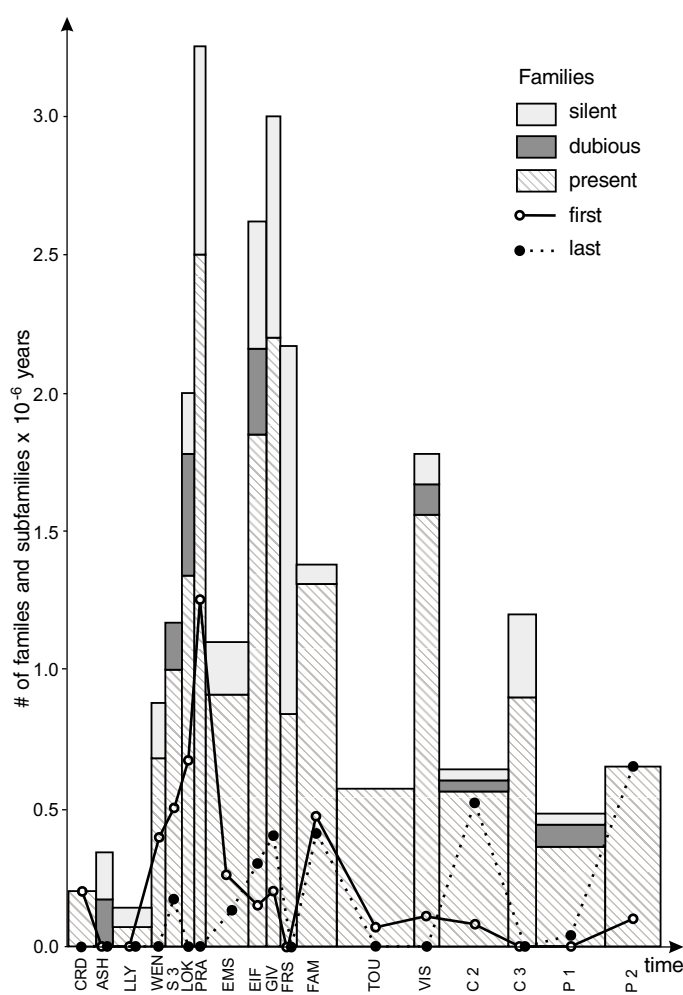


Fig. 1. Diversity of families and subfamilies of *Cyathaxonia* fauna, calculated per Ma, vs. series and stages of the Palaeozoic (bar diagram). Solid and dotted lines indicate respectively numbers of first and last records of (sub)families in each given interval. Analytical data are shown in Appendix 2, derived from Appendix 1. Data sources are indicated in explanations to Appendices 1 and 2.

(1989), the numbers of species suggest that there may have been approximately 50 genera in this interval. If this were so, the generic diversity per Ma during this interval would have been higher than during any of the Devonian intervals examined in this study.

Generally, the family level diversity shows that, after initially low levels in the Late Ordovician and the Early Silurian, periods of higher and lower diversities alternated throughout the rest of the Paleozoic.

Genus level data (Fig. 2, which is derived from the Appendix 4).—The general patterns seen in the generic record of diversity are similar to family level analysis, at least for the interval studied, i.e. for the Devonian. This validates the use of families rather than genera by Nudds and Sepkoski (1993) in their study of global diversity patterns of fossil Cnidaria. The similarities in family and genus diversities (Figs. 1 and 2) in-

dicate that the family level data of Hill (1981), the main source of information for Fig. 1, are to a large degree supported by the new genus level data, reported in numerous papers published during the last 20 years (as cited in remarks to Appendix 3). As in the family level analysis, significant differences exist between range through and raw data diversities in the Frasnian.

Fig. 2 shows similar patterns of diversity, to those seen in Fig. 1: sharp differences between the Pragian and Emsian, between the Givetian and Frasnian, and even a greater difference between the Famennian and the Tournaisian. Taking into consideration the ambiguous nature of “silent taxa”, the Frasnian diversity is either extremely different from the preceding Givetian (threefold decrease when raw data are considered) or very different (twofold decrease when range through data are used). On the other hand, the Frasnian–

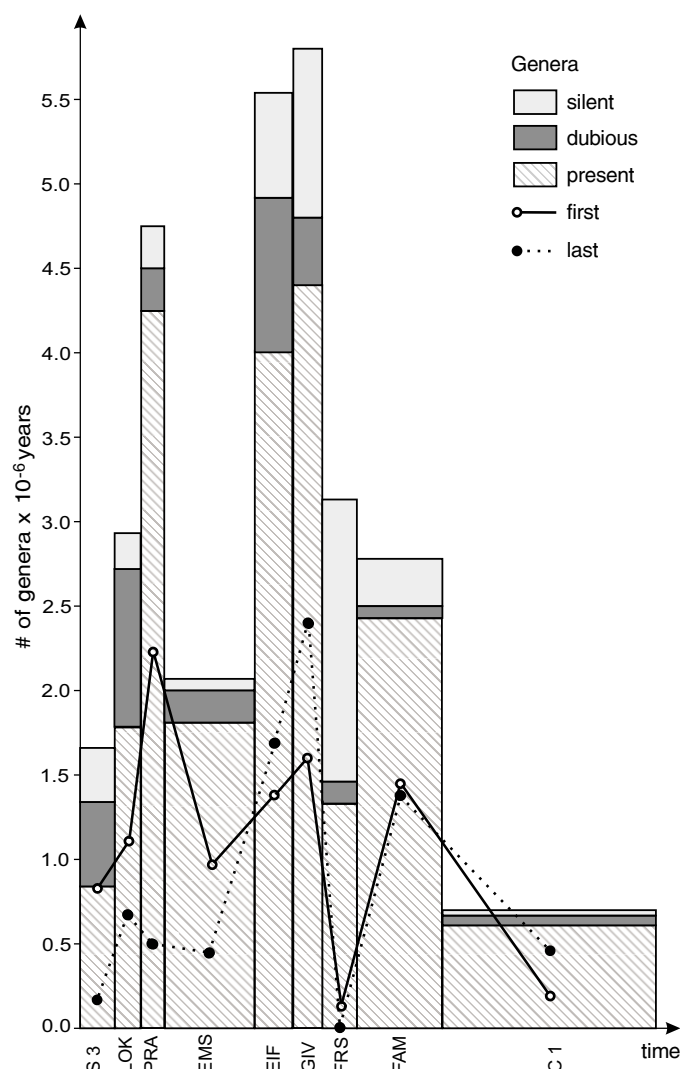


Fig. 2. Diversity of genera of *Cyathaxonia* fauna, calculated per Ma, in the Devonian; also data are added for the Upper Silurian and Lower Carboniferous. Solid and dotted lines indicate respectively first and last records of genera in each given interval. Analytical data are shown in Appendix 4, derived from Appendix 3. Data sources are indicated in explanations to Appendices 3 and 4.

Famennian comparison indicates either twofold increase in diversity (for raw data) or only a small decrease (for range through data).

Discussion

Silent taxa.—This is a new term introduced for those situations when supposedly monophyletic taxa are absent in significant intervals of their total range. Such barren intervals have been noted by other authors (e.g., Hill 1981, see also remarks in Sorauf 1989: 328; Olszewski and Patzkowsky 2001: 649–652). Olszewski and Patzkowsky (2001) discuss these absences in some detail. Although their study is regional rather than global and examines a narrower stratigraphic–chronologic interval than the present study, their general conclusions regarding missing taxa are applicable and may be summarized here. Olszewski and Patzkowsky (2001: 651–652) cite four possible reasons for absences, two of these indicate 1) poor knowledge of taxa in a given stratigraphic interval (a variety of causes can be suggested here) implying that the taxon actually existed during that time interval; usually a term “Lazarus” is used for such taxa; 2) the two other reasons for an absence cited by Olszewski and Patzkowsky indicate that the absence is sometimes “real” and the taxon was extinct in a given stratigraphic interval. Such “absences” are typically associated with “misidentification”, i.e., the polyphyletic nature of what was originally considered a monophyletic taxon (effect of iterative, or convergent evolution?). A term “Elvis” taxon is used for such taxa, mimicking the former ones. For supraspecific taxa, a combination of both explanations may explain a “silence”: some of the constituent species may belong to the Lazarus, the other to Elvis category. These missing records may be filled in the future by new discoveries of relevant faunas. Alternatively, data bases, such as these presented in Appendices 1 and 3, may be modified. For example the splitting of presently recognized taxa into several new ones may result in regrouping and recounting of first and last records. On the other hand, lumping of taxa currently falsely recognized as separate entities, will also affect diversity counts. Such taxonomic improvements are applicable to any group with a fossil record and all diversity studies must thus be viewed as provisional.

In this study, those taxa which are best candidates for these types of corrections are in the Petraiididae, Metriophyllidae, Lindstroemiidae and Pentaphyllinae. For each of these taxa three intervals of certain occurrence are recorded, separated by two intervals of silence. In an extreme case this would make 12 families (subfamilies) out of four recognized at present.

Varying stratigraphic schemes.—Diversity studies are influenced by the differences in stratigraphic usage and our ability to correlate. One example is the use of various hierarchical levels (series by Hill 1981, stages by Oliver and Pedder, 1979), the other is usage of various stratigraphic schemes at the same hierarchical level. For example, the terms Zlichovian and Couvinian were used by Oliver and Pedder (1979), whereas

other authors generally use Emsian and Eifelian. There is no simple correlation between these divisions, and in order to have the matter solved as precisely as possible, a detailed analysis of all relevant records should be undertaken to avoid errors (this has not been done in the present study).

Radiometric ages.—These data are extremely important to the conclusions of this study, especially for intervals of shortest duration: even minor absolute error is relatively significant in such cases. The reader is referred to error bars of the radiometric dating, as presented by McKerrow and Van Staal (2000: table 1).

Conclusions

Review of literature-based data indicates that the Devonian was a time of high diversity of the *Cyathaxonia* fauna, both in absolute numbers of (sub)families and genera during a given age and also with respect to numbers of taxa calculated for the duration of particular ages of this period. Emsian and Famennian faunas, although represented by the most numerous taxa, show low time-normalized diversities due to their more than average duration, whereas the shorter intervals of the Pragian and Givetian show the highest time-normalized diversities. Sharp differences (drops) in diversity are observed between the Pragian and Emsian, Givetian and Frasnian and Famennian and Tournaisian. The Frasnian *Cyathaxonia* fauna shows the lowest diversity at both (sub)family and genus levels of analysis. The post-Givetian crisis may have been responsible for this minimum, although the limited temporal resolution of this analysis does not allow for a more precise description of the Givetian–Frasnian and for the other transitions mentioned above.

However, in the Frasnian, silent taxa are extremely numerous in the *Cyathaxonia* fauna, i.e., taxa (both at the family-subfamily and at the genus level) which are present both prior to and after the Frasnian but are actually not recorded in the interval itself. These discontinuities in the fossil record may indicate either the Lazarus or Elvis taxa of the *Cyathaxonia* fauna in the Famennian: either the “Givetian” taxa remain so far undetected in the Frasnian or the “Famennian” taxa were newly evolved, and only superficially resemble the pre-Frasnian ones.

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Appendix 1

Stratigraphic record of families and subfamilies of *Cyathaxonia* fauna.

Stage	CRD	ASH	LLY	WEN	LUD	PRD	LOK	PRA	EMS	EIF	GIV	FRS	FAM	TOU	VIS	SPK	BSH	MOS	KAS	GZE	ASS	SAK	ART	KUN	UFI	KAZ	TAT
(Sub)family	+	?	1	1	1	1	1	0	=	?=																	
01 Palaeocyclidae	+	?	1	1	1	1	1	0	=	?=																	
02 Cyathaxoniidae					+	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	=	
03 Petraiidae	+	0	0	0	0	1	1	1	1	0	0	0	1	=													
04 Metriophyllidae				+	1	0	1	1	1	1	1	1	1	1	?	?	0	0	0	0	?	?	?	?	1	=	
05 Laccophyllinae				+	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	?	?	?	?	1	1	=
06 Guerichiphyllinae										?+	+	0	=														
07 Friedbergiinae													+=														
08 Neaxoniinae							+	1	1	1	1	1	1	1	1	=											
09 Taralasmatinae									+=																		
10 Amplexocariniinae							?+	+	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	=	?=
11 Kielcephyllidae													+=														
12 Lindstroemiidae								+	0	1	0	0	=														
13 Hadrophyllidae									+	1	=																
14 Combophyllidae									+	=																	
15 Stereolasmatidae								+	1	1	1	0	0	1	1	1	=	?=									
16 Antiphyllidae													+	1	1	1	1	1	1	1	1	1	=				
17 Hapsiphyllinae							+	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	=	
18 Adradosiinae								+	1	1	=																
19 Zaphrentoididae													+	1	1	1	1	1	1	1	0	0	0	0	1	=	
20 Polycoeliinae						?+	?	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	=	
21 Prosmiliinae																								+	1	=	
22 Anisophyllidae						+=																					
23 Pterophyllinae									+	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	=
24 Baryphyllinae														+	1	=											
25 Adamanophyllidae														+	1	=											
26 Pentaphyllinae								+	1	1	1	0	1	1	1	1	0	0	0	0	1	1	1	1	1	1	=
27 Commutiinae													+=														
28 Dalniinae													+=														
29 Lophophyllidae													+	1	1	1	1	1	1	1	1	1	1	1	1	=	
30 Timorphyllidae																									+=		
31 Verbeekiellidae															+	1	1	1	1	1	1	1	1	1	1	=	
Series/Stage	Ø2	Ø3	S1	S2	S3	LOK	PRA	EMS	EIF	GIV	FRS	FAM	TOU	VIS		C2		C3			P1				P2		
present* + absent	2+0	1+1	1+1	3+1	7+0	8+1	10+3	14+3	14+3	11+4	5+8	19+1	16+0	15+1		15+1		9+3			11+1				13+0		
first + last	2+0	0+0	0+0	2+0	3+1	3+0	5+0	4+2	1+2	1+2	0+0	7+6	2+0	1+0		2+13		0+0			0+1				2+13		

Explanations.—Stages abbreviated as in Nudds and Sepkoski (1993); records: +, first (?+ questionable first); 1, present; ?, dubious; 0, silent; =, last (?= questionable last); * “present” records include also “dubious” ones.

Appendix 2

Summarized stratigraphic distribution and diversity of families and subfamilies of *Cyathaxonia* fauna.

Strati- -graphy	Time in 10 ⁶ years	Records						
		total			first		last	
			dubious	silent		dubious		dubious
CRD	10	2 / 0.2	0 / 0	0 / 0	2 / 0.2	0 / 0	0 / 0	0 / 0
ASH	6	2 / 0.33	1 / 0.17	1 / 0.17	0 / 0	0 / 0	0 / 0	0 / 0
LLY	14	2 / 0.14	0 / 0	1 / 0.07	0 / 0	0 / 0	0 / 0	0 / 0
WEN	5	4 / 0.8	0 / 0	1 / 0.2	2 / 0.4	0 / 0	0 / 0	0 / 0
S3	6	7 / 1.17	1 / 0.17	0 / 0	3 / 0.5	1 / 0.17	1 / 0.17	0 / 0
LOK	4.5	9 / 2.0	2 / 0.44	1 / 0.22	3 / 0.67	1 / 0.22	0 / 0	0 / 0
PRA	4	13 / 3.25	0 / 0	3 / 0.75	5 / 1.25	0 / 0	0 / 0	0 / 0
EMS	15.5	17 / 1.1	0 / 0	3 / 0.19	4 / 0.26	0 / 0	2 / 0.13	0 / 0
EIF	6.5	17 / 2.62	2 / 0.31	3 / 0.46	1 / 0.15	1 / 0.15	2 / 0.31	1 / 0.15
GIV	5	15 / 3.0	0 / 0	4 / 0.8	1 / 0.2	0 / 0	2 / 0.4	0 / 0
FRS	6	13 / 2.17	0 / 0	8 / 1.33	0 / 0	0 / 0	0 / 0	0 / 0
FAM	14.5	20 / 1.38	0 / 0	1 / 0.07	7 / 0.48	0 / 0	6 / 0.41	0 / 0
TOU	28	16 / 0.57	0 / 0	0 / 0	2 / 0.07	0 / 0	0 / 0	0 / 0
VIS	9	16 / 1.78	1 / 0.11	1 / 0.11	1 / 0.11	0 / 0	0 / 0	0 / 0
C2	25	16 / 0.64	1 / 0.04	1 / 0.04	2 / 0.08	0 / 0	13 / 0.52	0 / 0
C3	10	12 / 1.2	0 / 0	3 / 0.3	0 / 0	0 / 0	0 / 0	0 / 0
P1	25	12 / 0.48	2 / 0.08	1 / 0.04	0 / 0	0 / 0	1 / 0.04	0 / 0
P2	20	13 / 0.65	0 / 0	0 / 0	2 / 0.1	0 / 0	13 / 0.65	0 / 0

Explanations.—Time, taken from McKerrow and Van Staal (2000). Records, taken from Appendix 1: first numbers—actual numbers of taxa recorded; second numbers (diversities per Ma) calculated from the first ones divided by time.

Appendix 3

Stratigraphic distribution of Devonian genera of *Cyathaxonia* fauna.

fam	genus	+	S3	LOK	PRA	EMS	EIF	GIV	FRS	FAM	C1	=	remarks
01	<i>Boiocyclus</i>					+=	=?						18
01	<i>Rhabdocyclus</i>	S1	1	=									
02	<i>Cyathaxonia</i>									+	1	P2	
03	<i>Petraia</i>		+	1	1	0	0	0	0	=			(8),24
03	<i>Haptophyllum</i>					+=							
03	<i>Petraiella</i>									+=			
03	<i>Thuriantha</i>										+		19
04	<i>Metriophyllum</i>				+	1	1	1	1	1	1	P1?	(8,10,13)
04	<i>Bathybalva</i>										+=		19
04	<i>Duncanella</i>	S2	0	1	1	1	=						20
04	<i>Metrioplexus</i>						=	0	0	=			9
04	<i>Petronella</i>					+	=						
04?	<i>Gymnaxon</i>					+=							1
04?	<i>Pseudopetraia</i>				+	1	1	=					22
05	<i>Laccophyllum</i>	S2	0	1	1	1	1	1	0	0	=		23
05	<i>Alleynia</i>						+=						
05	<i>Barrandeophyllum</i>					+	+	0	0	=			(8,11,14)
05	<i>Bitraia</i>						+=						
05	<i>Boolelasma</i>				+	1	0	=					
05	<i>Metronaxon</i>				+	1	1	=					
05	<i>Pedderelasma</i>						+=						
05	<i>Saucrophyllum</i>			+	?	=?							
05	<i>Schindewolfia</i>		+	+	0	1	0	=					2
05	<i>Sutherlandinia</i>	S2	1	0	=								16
05	<i>Syringaxon</i>	S1	1	1	1	1	1	1	1	=			9
06	<i>Guerrichiphyllum</i>						+	+	0	=			
07	<i>Friedbergia</i>									+=			
08	<i>Neaxon</i>			+	1	1	1	1	0	1	=		
08	<i>Catactotoechus</i>						+	+	1	=			5
08	<i>Czarnockia</i>									+=			
08	<i>Hillaxon</i>									+=			
08	<i>Neaxonella</i>					+=							
09	<i>Taralasma</i>					+=							
10	<i>Amplexocarinia</i>									+	1	P	
10	<i>Gorizdronia</i>									+=			
10	<i>Naltvkinella</i>					+	1	0	1	=			(8)
10	<i>Nicholsoniella</i>				+	1	1	1	1	=			(13)
10?	<i>Retiophyllum</i>			+	1	=?	=?						
11	<i>Kielcephyllum</i>									+=			
11	<i>Kozłowskiinia</i>									+=			
11	<i>Thecaxon</i>								+	=			17
12	<i>Famaxonina</i>									+=			
12	<i>Rhipidophyllum</i>				+=								
12	<i>Ridderia</i>						+=						
13	<i>Hadrophyllum</i>					+	1	=					
13	<i>Crassicycclus</i>						+=						
13	<i>Microcycclus</i>					+	1	=					12
14	<i>Combophyllum</i>					+	=						
15	<i>Stereolasma</i>			+	1	1	=						
15	<i>Amplexiphyllum</i>				+	0	=						
15	<i>Drewerelasma</i>									+=			15
15	<i>Lopholasma</i>							+	0	0	+=	C2?	
15	<i>Saleelasma</i>									+=			
15	<i>Stewartophyllum</i>					+	1	=					
16	<i>Bradyphyllum</i>									+	0	C2	
16	<i>Pseudoclaviphyllum</i>									+	=		
17	<i>"Hapsiphyllum"</i>			+	1	1	1	1	0	0	=		
17	<i>Famennelasma</i>						+	1	=				2
17	<i>Zaphrentites</i>						+	+	0	1	1	C2	(8)
18	<i>Adradosia</i>				+	1	1	=					2,3,21
18	<i>Brevisseptosia</i>							+=					2
19	<i>Zaphrentoides</i>									+	=		(6,8)
19	<i>Amplexizaphrentis</i>									+	=		(6)
20	<i>Amandaraia</i>		+	=?									
20	<i>Calophyllum</i>									+	?	P	
20	<i>Sochkineophyllum</i>									+=			
22	<i>Anisophyllum</i>		+=										
23	<i>Plerophyllum</i>									+	0	P2	
23	<i>Ufimia</i>					+	1	1	0	1	1	P2	
24	<i>Baryphyllum</i>										+=		
24	<i>Barylasma</i>										+=		
25	<i>Tachyphyllum</i>										+=		
26	<i>Pentaphyllum</i>					+	1	0	1	0	1	P2?	
26	<i>Antikinkaidia</i>									+	=		
26	<i>Oligophyllum</i>				+	1	1	=	?	=?			
27	<i>Communia</i>									+	=		
28	<i>Dalnia</i>									+	=		
29	<i>Lophophyllum</i>									+	=		(6)
??	<i>Kitakamiphyllum</i>		+	=?									

Explanations.—Taxonomy: family numbers as in Appendix 1. Genera: the Devonian ones are listed, but additionally those which are present in the Upper Silurian and/or in the Lower Carboniferous. Records: symbols as explained by Appendix 1. Remarks: data sources as follows (numbers in parentheses refer to non-illustrated material); 1, Birenheide and Soto 1977; 2, Birenheide and Soto 1992; 3, Grigo et al. 1992; 4, Hill 1981; 5, Lütte and Galle 1989; 6, Nudds and Sepkoski 1993; 7, Oliver and Pedder 1979; 8, Pedder 1982; 9, Rózkowska 1969; 10, Scrutton 1988; 11, Soto 1979; 12, Soto 1983; 13, Soto and Lin 1997; 14, Weyer 1973a; 15, Weyer 1973b; 16, Weyer 1978a; 17, Weyer 1978b; 18, Weyer 1981a; 19, Weyer 1981b; 20, Weyer 1984; 21, Weyer 1985; 22, Weyer 1991a; 23, Weyer 1991b; 24, Weyer 2000.

Appendix 4

Summarized stratigraphic distribution and diversity of Devonian genera of *Cyathaxonia* fauna.

Stratigraphy	Time in 10 ⁶ years	Records						
		total			first		last	
			dubious	silent		dubious		dubious
S3	6	10 / 1.67	3 / 0.5	2 / 0.33	5 / 0.83	3 / 0.5	1 / 0.17	0 / 0
LOK	4.5	13 / 2.89	4 / 0.89	1 / 0.22	5 / 1.11	2 / 0.44	3 / 0.67	2 / 0.44
PRA	4	19 / 4.75	1 / 0.25	1 / 0.25	9 / 2.25	0 / 0	2 / 0.5	0 / 0
EMS	15.5	32 / 2.06	3 / 0.19	1 / 0.06	15 / 0.97	1 / 0.06	7 / 0.45	2 / 0.13
EIF	6.5	36 / 5.54	6 / 0.92	4 / 0.62	9 / 1.38	4 / 0.62	11 / 1.69	2 / 0.31
GIV	5	29 / 5.8	2 / 0.4	5 / 1.0	6 / 1.2	2 / 0.4	12 / 2.4	0 / 0
FRS	6	19 / 3.17	1 / 0.17	10 / 1.67	1 / 0.17	0 / 0	0 / 0	0 / 0
FAM	14.5	40 / 2.76	1 / 0.07	4 / 0.28	21 / 1.45	0 / 0	20 / 1.38	1 / 0.07
C1	37	26 / 0.7	2 / 0.06	1 / 0.03	7 / 0.19	0 / 0	17 / 0.46	1 / 0.03

Explanations.—Stratigraphy: besides the Devonian stages also the Upper Silurian and Lower Carboniferous series are included for comparison. Time: data taken from McKerrow and Van Staal (2000); records: first numbers taken from Appendix 3, refer to absolute numbers of genera; second numbers (generic diversity per Ma) were calculated by dividing first numbers over duration of a particular interval.